Development of the PCAD Model to Assess Biological Significance of Acoustic Disturbance

Daniel P. Costa Professor of Ecology and Evolutionary Biology University of California Santa Cruz, CA 95060

phone: (831) 459-2786 fax: (831) 459-3383 email: costa@ucsc.edu

Award Number: N00014-13-1-0134 http://bio.research.ucsc.edu/people/costa/

LONG-TERM GOALS

Assessing the impact of disturbance events on cryptic or far-ranging marine mammal species is critically important to stakeholders who must balance project objectives with the environmental impacts of proposed activities. In recent years, considerable scientific interest in this topic has led to key discoveries relating to species-specific sensitivities, behavioral responses, and the physics of disturbance; however, we still lack the ability to predict the effect of potential disturbance events on a population. To better inform stakeholders about the likely consequences of a specific proposed activity, the PCAD (Population Consequences of Acoustic Disturbance) working group established a conceptual framework detailing the impact of disturbance events and how the effects cascade from individuals altering their behavior all the way to population-level demographic effects. The PCAD working group then developed a more rigorous analytical approach (New et al. 2014). These methods require substantial pre-existing knowledge of foraging patterns, life-history schedules, and demographics. Therefore, it is essential to use well-studied species to validate the approach. This is best accomplished by selecting species that are as similar as possible to target species and are also extremely well-studied. We identified northern elephant seals and Atlantic bottlenose dolphins as the best species to parameterize the PCAD model. These species represent two life-history extremes (capital and income breeders), have clear taxonomic separation (pinnipeds and cetaceans), and both species have been studied intensively for several decades, providing unprecedented demographic data. These factors imply that they likely respond to disturbance in unique ways and by developing models for each system, we can effectively bound the input parameters (and expected outputs) for other species of interest. This will be an essential step to eventually apply the model to species for which much less is known.

In the current project, we are focusing on several key opportunities. First, the combination of remarkable demographic data with "health" or body condition data will allow us for the first time to assess the effects of a disturbance event through all of the transfer functions of the PCAD model. This will be done with both simulated, natural, and experimental disturbance events, giving us the power to estimate the effects of proposed disturbance activities while bounding the estimates with real-world values. We will also be focusing on some of the mechanistic aspects of the PCAD model. For example, by investigating fine-scale energetics via accelerometry or the role of the stress response in long-term

health and reproduction, we can begin developing tools that will enhance our confidence in the PCAD model for the data-limiting/cryptic species.

OBJECTIVES

While considerable progress has been made to quantify the transfer functions described above for southern elephant seals, our goals are to parameterize these models to make them applicable to other species and take the models one step further by simulating disturbances and quantifying how such disturbances may affect the population. Although this three-year project encompasses many aspects of the PCAD effort, we list only the objectives we have worked on during this second year.

- 1. Analysis of northern elephant seal demographic data to estimate adult female survival, reproduction, and pup survival as a function of maternal condition. As a major part of this effort, we completed a study to compare our method for assessing body composition in the northern elephant seal (truncated cones) with labeled water techniques. This enables us to quantify the uncertainty associated with female condition metrics (lipid mass) that is a key link between disturbance events and demographic rates.
- 2. Determine the ability of elephant seals to modify their foraging behavior (i.e. dive depth, dive frequency, trip duration, etc) to compensate for lost foraging opportunities, quantifying their resilience to disturbance. Specifically, analyze recently collected accelerometer data to estimate the energetic cost of displacement away from a disturbance.
- 3. Organize and then incorporate Dr. Randy Wells' Sarasota Bay dolphin data set for analysis of an income breeding system.

APPROACH

Body Composition Comparison Study

Quantified uncertainty is becoming a standard metric provided to policy makers when deciding on protection levels for species (Regan et al. 2013). If physiological indicators are to become a part of models to predict the population outcome of disturbance, it is important to quantify the uncertainty in those metrics. In particular, lipid mass of female elephant seals has become a critical foraging success metric linked to reproductive rate. Pups' wean mass is also a function of maternal condition, and wean mass affects pup survival (McMahon et al. 2000, Crocker et al. 2001). To better understand the uncertainty in lipid mass estimates, this study compared results of several different methods to estimate percent lipid in elephant seals: elliptical truncated cones, circular truncated cones, and labeled water. We included use of two different ultrasound machines (with and without images), accounted for the proportion lipid in skin, and quantified uncertainty in all techniques.

Energetic Cost of Displacement

To understand the energetic cost of displacement, it is first necessary to understand how animals function normally. Specifically, quantifying the balance between how much food energy an individual requires to perform necessary life functions, and how much energy it expends in acquiring it, allows us to establish a physiological 'baseline' against which to compare the energetic costs associated with any changes in behavior. The next step is to then simulate disturbance, and measure the magnitudes of the behavioral and energetic avoidance responses – i.e., how did behavior change, and what were the associated energetic costs of those changes?

Sarasota Bay Bottlenose Dolphin Analysis

The first step to analyzing the bottlenose dolphin data is to create a mark-recapture model to estimate survival and reproductive rates. We have used a Bayesian Cormack-Jolly-Seber model based on resights of animals both in and out of the main study area (Schwarz et al. 2013), limited to animals that are found within the main study area during at least 50% of the year (resident population). Given seasonal differences in calving, causes of mortality, and movement patterns, we estimated survival rates on a quarterly basis, and mother-calf separation and calving rates on an annual basis from May 1, 1992 through April 30, 2010 (latest available data). Another important aspect of this research is to find easy-to-measure physiological metrics that can be applied to dolphin populations. We have investigated survival and mother-calf separation as a function of body mass index (BMI) and proportion lipid in blubber. We have also quantified the relationship between those metrics and red tide as well as caloric content of prey fish sets during later years.

WORK COMPLETED

Body Composition Comparison Study

During Year 1 of this contract, we collected both morphometric and tritiated water data from ten adult female seals. In year 2, we collected and analyzed data on skin thickness (N = 46) and proportion lipid content in both skin (N = 3) and blubber (N = 26) to estimate the proportion of total lipid found in those tissues. This work was published in the summer of 2015.

Schwarz, L. K., S. Villegas-Amtmann, R. S. Beltran, D. P. Costa, C. Goetsch, L. Hückstädt, J. L. Maresh, S. H. Peterson. (2015) Comparisons and uncertainty in fat and adipose tissue estimation techniques: the northern elephant seal as a case study. PLoS ONE 10(6): e0131877. doi:10.1371/journal.pone.0131877

Energetic Cost of Displacement

To quantify the at-sea physiology of northern elephant seals under both normal and disturbed conditions, we used a two-stepped approach. First, we used a translocation paradigm (Andrews et al. 1997, Oliver et al. 1998, Webb et al. 1998, Costa et al. 2003) and the doubly-labeled water method (Nagy 1983, Costa 1987, Speakman 1997, Sparling et al. 2008) to measure the at-sea cost of locomotion in 12 juvenile seals (Maresh et al. 2014). Then, we were able to apply this knowledge to 23 adult female seals tagged with accelerometers that monitored fine-scale locomotion behavior. Collectively, this information allowed us to construct activity-energy budgets for elephant seals during their foraging migrations, giving us insight into not only their energy requirments, but also into the foraging behaviors that allow them to stay in positive energy balance.

During the studies on both juveniles and adult seals, we were able to simulate disturbance by tagging some individuals (juveniles N = 11, adults N = 3) with instrumentation that artificially increased transport costs, thereby causing increased swimming effort in ways that are comparable to those measured under scenarios of decreased prey availability under standard locomotion (Cornick et al. 2006). Our studies were unique in their ability to couple both behavioral and energetic measurements on wild animals *in situ*.

Work describing the ability of elephant seals to modify their foraging behavior to compensate for lost foraging opportunities, and quantification of their resilience to at-sea disturbance, has been completed. During the past year, revisions to the final manuscripts were completed and the papers were accepted for publication (see citations below).

Maresh, J.L., S.E. Simmons, D.E. Crocker, B.I. McDonald, T.M. Williams, D.P. Costa. 2014. Free-swimming northern elephant seals have low field metabolic rates that are sensitive to an increased cost of transport. Journal of Experimental Biology 217(9): 1485-1495.

Maresh, J.L., T. Adachi, A. Takahashi, Y. Naito, D.E. Crocker, T.M. Williams, M. Horning, D.P. Costa (in press). Summing the strokes: energy economy in northern elephant seals during large-scale migrations. Movement Ecology: doi 10.1186/s40462-015-0049-2.

Sarasota Bay Bottlenose Dolphin Analysis

In March 2014, Dr. Randy Wells provided quarterly mark-recapture data to Dr. Lisa Schwarz on 134 females, 122 males, and 80 of unknown sex. We have investigated survival, reproduction, and mother-calf separation as a function of age and an annual red tide index using a Bayesian Cormack-Jolly-Seber mark-recapture model. Quarterly movement probabilities in and out of the area were estimated by year. In August 2015, Dr. Wells provided fish prey net capture data as well as annual health metric data from health assessments (body mass index, white blood cell count, proportion lipid in blubber) to compare with annual survival rate estimates and red tide.

RESULTS

Body Composition Comparison Study

We showed that Northern elephant seals are elliptical on land, rather than the assumed circular shape, and skin may account for a high proportion of what is often defined as blubber. Also, blubber extends past the neck-to-pelvis region, and comparisons of new and old ultrasound instrumentation indicate previous measurements of sculp thickness may be biased low. Accounting for such differences, and incorporating new measurements of blubber density and proportion of fat in blubber, we proposed a modified cones method that can isolate blubber from non-blubber adipose tissue and separate fat into skin, blubber, and core compartments. Lastly, we found that adipose tissue and fat estimates using tritiated water may be biased high during the early molt. Both the tritiated water and modified cones methods had high, but reducible, uncertainty. The improved cones method for estimating body condition allows for more accurate quantification of the various tissue masses and may also be transferrable to other species.

Energetic Cost of Displacement

In our study on translocated juveniles, we found that the cost of each flipper stroke (Williams et al. 2004) during standard locomotion was approximately 2.58 J kg⁻¹. Field metabolic rates were 122.5 kJ kg⁻¹ day⁻¹ and 79.8 kJ kg⁻¹ day⁻¹ for one- and two-year-old seals, respectively. Energetically, elephant seals were sensitive to increased transport costs, with the cost per stroke increasing by 71% and the field metabolic rate increasing by 60% under the disturbance scenario. These extra costs were reflected in changes in some of their diving behaviors, most notably a 46% increase in time spent at the surface resting between dives.

In our study on adult females, we found that elephant seals have low field metabolic rates (mean = 73.6 kJ kg⁻¹ d⁻¹ and 56.1 kJ kg⁻¹ d⁻¹ during their short and long migrations, respectively; Fig. 1) that are maintained to some extent by keeping locomotion costs low – elephant seals allocated only 4% of totally energy intake towards fueling locomotion (Fig. 2). For the three individuals carrying the extra instrumentation, the increased swimming effort increased locomotion costs by 400% (Fig. 2), and overall FMRs increased by 22%. Seals under the simulated disturbance scenario allocated roughly 16% of total energy intake towards locomotion, enough to upset energy balance in these individuals. Seals

under the drag scenario were only able to allocate one-third as much of their prey energy intake toward their own growth compared to seals swimming without the added transport costs, and these individuals returned from their foraging migrations noticeably undersized and nutritionally stressed. Extra costs under the disturbance scenario were reflected behaviorally as a 25% increase in flipper stroking rate (Fig. 3) and, for one individual, extended time spent at sea.

Sarasota Bay Bottlenose Dolphin Analysis

A simple model separating rates by age classes (1 year, 2-7 years, and 8+ years old) resulted in the best fit to the data and produced similar population growth rate estimates compared to more complex age-structured models. Male and female bottlenose dolphins have similar survival rates by age. Movement patterns indicate a general move in to the main study area in 1996 and 1997, coincident with the ban on net fishing. During a severe red tide event in 2005, resident animals were less likely to move in to and more likely to move out of the main study area. Mother-calf separation increases as the duration of severe red tides increase. Annual survival rates for both 2-7 year olds and 8+ year olds are correlated with red tide events the previous year in Sarasota Bay (N = 14 years). Preliminary analysis shows surviving animals exhibit a decline in proportion lipid in the blubber when survival rates are lower (N = 10 years). The change in proportion lipid in blubber may also be correlated with red tide intensity the previous year; however, sample size was not large enough to show a statistically strong connection (N = 10 years, representing 5 red tide values). Sample size was also too small to determine the relationship between proportion lipid in blubber and annual prey caloric availability (MJ/set; N = 3 years). However, there was a decline in winter MJ/set with increased red tide duration. Body Mass Index was not a good indicator of annual fluctuations in population health, was not correlated with survival or mother-calf separation rates, and did not change as a function of severe red tide duration.

IMPACT/APPLICATIONS

Body Composition Comparison Study

Lipid mass and body condition are important metrics in bioenergetics and physiological studies. They can also link foraging success and demographic rates, making them key components of models that predict population-level outcomes of environmental change. Therefore, it is important to incorporate uncertainty in physiological indicators if results will lead to species management decisions. Results indicate that future research should incorporate uncertainty in this important physiological metric and should account for skin properties and elliptical shape when using the truncated cones method.

Energetic Cost of Displacement

We found that anthropogenic disturbance of wild northern elephant seals via increased locomoation costs (as in, for example, avoidance behaviors) can have serious impacts on behavior and foraging success in this species. This is notable given that elephant seals generally are considered to be a relatively hearty species compared to other marine mammals. These results suggest that more sensitive species should be expected to experience the effects of at-sea disturbance more severely.

Sarasota Bay Bottlenose Dolphin Analysis

Using red tide as a metric for disturbance will allow us to complete a PCAD model for bottlenose dolphins based on unique, long-term empirical data. The results of this analysis will aid in understanding the relationships we might see for species, or other bottlenose dolphin populations, for which we have very little data and may aid in determining the most effective type of data to collect to determine the population consequences of disturbance.

RELATED PROJECTS

- Application of the PCAD Model to the California Gray Whale, Integration of Existing Data and Towards a Quantitative Assessment of Biological Significance of Acoustic Disturbance. Joint Award Shell Oil and ExxonMobil Oil Companies. Nov 1 2012-Sept 31 2013. \$120,000.
- Environmental perturbations, behavioral change, and population response in a long-term northern elephant seal study. ONR N00014-10-1-0356.
- A bioenergetic model to estimate the population consequences of disturbance. The E&P Sound and Marine Life Joint Industry Programme. September 2014 August 2017. \$1,050,780.

REFERENCES

- Andrews, R. D., D. R. Jones, , J. D. Williams, P. H. Thorson, G. W. Oliver, D. P. Costa, and B. J. LeBoeuf. 1997. Heart rates of northern elephant seals diving at sea and resting on the beach. Journal of Experimental Biology 200:2083-2095.
- Cornick, L. A., S. D. Inglis, K. Willis, and M. Horning. 2006. Effects of increased swimming costs on foraging behavior and efficiency of captive Steller sea lions: evidence for behavioral plasticity in the recovery phase of dives. Journal of Experimental Marine Biology and Ecology 333:306-314.
- Costa, D. P. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. In Approaches to Marine Mammal Energetics, Vol. 1, pp. 43-66.
- Costa, D. P., D. E. Crocker, J. Gedamke, P. M. Webb, D. S. Houser, S. B. Blackwell, D. Waples, S. A. Hayes and B. J. Le Boeuf. 2003. The effect of a low-frequency sound source (acoustic thermometry of the ocean climate) on the diving behavior of juvenile northern elephant seals, *Mirounga angustirostris*. Journal of the Acoustic Society of America 113:1155-1165.
- Costa, D. P., L. K. Schwarz, P. W. Robinson, R. S. Schick, P. A. Morris, R. S. Condit, D. E. Crocker, and A. M. Kilpatrick. In press. A bioenergetics approach to understanding population consequences of disturbance: elephant seals as a model system. The Effects of Noise on Aquatic Life II. Springer.
- Crocker, D. E., J. D. Williams, D. P. Costa, and B. J. Le Boeuf. 2001. Maternal traits and reproductive effort in northern elephant seals. Ecology 82:3541-3555.
- Maresh, J. L., S. E. Simmons, D. E. Crocker, B. I. McDonald, T. M. Williams, and D. P. Costa. 2014. Free-swimming northern elephant seals have low field metabolic rates that are sensitive to an increased cost of transport. Journal of Experimental Biology (in press).
- Maresh, J. L., T. Adachi, A. Takahashi, Y. Naito, D. E. Crocker, T. M. Williams, and D. P. Costa (in review). Summing the strokes: extreme energy economy in a large marine carnivore. Functional Ecology
- McMahon, C. R., H. R. Burton, and M. N. Bester. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. Antarctic Science 12:149-153.
- Nagy, K. A. (1983). The Doubly Labeled Water (3HH18O) Method: A Guide to its Use. Los Angeles: UCLA Publ. No. 12-1417

- New, L. F., J. S. Clark, D. P. Costa, E. Fleishman, M. A. Hindell, T. Klanjšček, D. Lusseau, S. Kraus, C. R. McMahon, P. W. Robinson, R. S. Schick, L. K. Schwarz, S. E. Simmons, L. Thomas, P. Tyack, and J. Harwood. 2014. Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Marine Ecology Progress Series 496:99 108.
- Oliver, G. W., P. A. Morris, P. H. Thorson, and B. J. Le Boeuf. 1998. Homing behavior of juvenile northern elephant seals. Marine Mammal Science 14:245-256.
- Regan, T. J., B. L. Taylor, G. G. Thompson, J. F. Cochrane, K. Ralls, M. C. Runge, and R. Merrick. 2013. Testing Decision Rules for Categorizing Species' Extinction Risk to Help Develop Quantitative Listing Criteria for the US Endangered Species Act. Conservation Biology 27:821-831.
- Schwarz, L. K., M. Goebel, D. Costa, and A. M. Kilpatrick. 2013. Top-down and bottom-up influences on demographic rates of Antarctic fur seals (*Arctocephalus gazella*). Journal of Animal Ecology 82:903 911.
- Sparling, C. E., D. Thompson, M. A. Fedak, S. L. Gallon, and J. R. Speakman. 2008. Estimating field metabolic rates of pinnipeds: doubly labelled water gets the seal of approval. Functional Ecology 22:245-254.
- Speakman, J. R. 1997. Doubly Labelled Water: Theory and Practice. London; New York: Chapman & Hall
- Webb, P. M., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998b. Effects of buoyancy on the diving behavior of northern elephant seals. Journal of Experimental Biology 201:2349-2358.
- Williams, T. M., L. A. Fuiman, M. Horning, and R. W. Davis. 2004a. The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. Journal of Experimental Biology 207:973-982.